THE GROWTH OF *SPHAGNUM*: METHODS OF MEASUREMENT

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INTRODUCTION

Peat covers a large part of the earth's land surface to the north of 60°N latitude (map in Sjörs 1961). In Finland, for example, about a third of the land is peat covered. South of 60°N peat is still locally abundant. A conservative estimate puts the area covered by peat at about 1% of the total land surface of the earth (Taylor 1964). *Sphagnum* plants are, by mass, probably amongst the principal peat formers. Any attempt to account for the rate of peat formation, or for peat stratigraphy and present surface features, is therefore likely to require information on the rate of *Sphagnum* growth.

Some special features of Sphagnum *of importance in growth studies*

Sphagnum has several features which are rare or absent in vascular plants, and which might be expected to affect the efficiency of dry matter production. The plants are able to flourish in habitats in which there are uncommonly low concentrations of inorganic solutes, particularly of N and P compounds. The concentration of these in the plants mirrors that in the habitat; 0·6% N and 0·03% P by weight are reported by Malmer & Sjörs (1955). The habitats are, moreover, often unusually acid; pH values below 4 are frequent.

The structure of *Sphagnum* is unusual. Approximately two-thirds of the dry matter of the plants is in the leaves. Most of the chlorophyll is contained in an open network of long narrow cells which adjoin other chlorophyllose cells only at the ends. The intervening empty cells have relatively large pores (5–15 μ diameter) and the leaves are only one cell thick, so that each chlorophyll-containing cell is effectively freely suspended but is held in a structure of fixed form. *Sphagnum* is, therefore, intermediate between a planktonic algal population and a vascular plant, not only in distribution of chlorophyllose cells but also in dependence on liquid water and perhaps limitation by the relatively low rate of CO_2 diffusion in water.

A Sphagnum community is, in some respects, a very convenient experimental unit. Individual species occur in different ranges of chemical conditions in the habitat; *S. squarrosum** may be found in moderately calcareous conditions, whilst *S. papillosum* thrives only in places where the calcium concentration is low. Species differ too in tolerance of drier conditions; *S. cuspidatum* rarely occurs more than a few centimetres above the water table, whilst *S. rubellum* is usually found in drier places.

The plants are easily handled, and usually grow with their stems nearly parallel to one another. There are no roots, so that there is no difficulty in estimating the amount of underground parts, which can form an appreciable part of higher plant production (Westlake 1963).

* Nomenclature follows Richards & Wallace (1950).

Growth is predominantly apical and indeterminate, so that the main axis in space is also an axis in time.

Lastly, since the plants are primarily aquatic, experiments may be made in water culture, with all its advantages over mixed solid/liquid culture, with some hope that the results may be relevant to field behaviour.

In other respects this system is less convenient. One of the main difficulties, arising from the growth habit, is that boundaries between parts of the plant are either uncertain or inconvenient. It is rare, for example, to find a sharp boundary between live and dead parts of the plants, or even on a practical basis between green and brown parts. The sharpest divisions are of leaf from branch, which provides inconveniently small units. More useful practical divisions are of branches (with attached leaves) from stem, and of capitulum from the rest of the plant.

The amount of growth is an important parameter in any attempt to account for the concentration of cations, and particularly of H^+, around the plants (Clymo 1967). During a period of growth the number of new ion exchange sites (and probably the amount of exchangeable H^+ too) are directly related to the amount of dry matter produced. The reported values for growth vary from 0·77 g dm^{-2} $year^{-1}$ (for a mixture of *S. papillosum* and *S. magellanicum* at 300 m altitude in northern England; Chapman 1965) to 16·6 g dm^{-2} $year^{-1}$ (for *S. recurvum* in northern Germany; Overbeck & Happach 1956).

The meaning attached here to growth

The term 'production', with its allies and derivatives, is acquiring a fairly precise meaning. Growth appears to be no nearer an agreed definition than ever it was, though an element of irreversible increase is usually involved. The methods to be described here do not all measure the same thing, and cannot always be related to the production terms, though most are concerned with an increase of some kind. Growth is used as a neutral term for all the quantities measured here.

Because there is no clear division between live plant, dead plant and peat, the terms 'standing crop' and 'biomass' have no useful meaning when applied to *Sphagnum*.

The measurement of growth

The main problem in measuring anything as complex as growth, particularly in field conditions, is that there is no yardstick with which to assess accuracy. Precision of any one method may be estimated with standard statistical techniques, but a highly precise estimate is not necessarily highly accurate; in the game of darts the shots may be close together but all a long way from the point aimed at. Close agreement between mean results is then the best evidence of accuracy. The more diverse the methods, the better their mutual support.

In this paper the methods available for measuring *Sphagnum* growth are first described, with notes on their range of application. Tests of the more promising methods are considered next. These tests include some in field conditions. The limitations revealed in these tests are discussed as they occur.

Conversion of results to an area basis needs additional measurements, and these are considered next. Lastly are discussed the constancy of *Sphagnum* carpet density, the bearing of the results on estimates of accumulation, and the efficiency of a *Sphagnum* carpet.

METHODS OF MEASURING GROWTH

In order to compare methods of measuring growth in mass it is useful to refer to a simple model system (Fig. 1). The boundaries in this model are the outer surface of the plant, and a specified time interval, since growth will not usually be at a constant rate. A particular atom may, during the course of the experiment, pass one or more times between the compartments. For example, a carbon atom might be assimilated by a live cell during the day, released by respiration at night, and reassimilated the next day by another leaf. Only its positions at the beginning and end of the experiment matter. An amount of material α is present at the start of the experimental period. During the experiment an amount β of growth is made. This corresponds to gross primary production. During the same time there are losses: α_r and β_r due to self destructive processes (mainly 'apparent respiration'), α_p and β_p due to 'predation', including losses due to animal

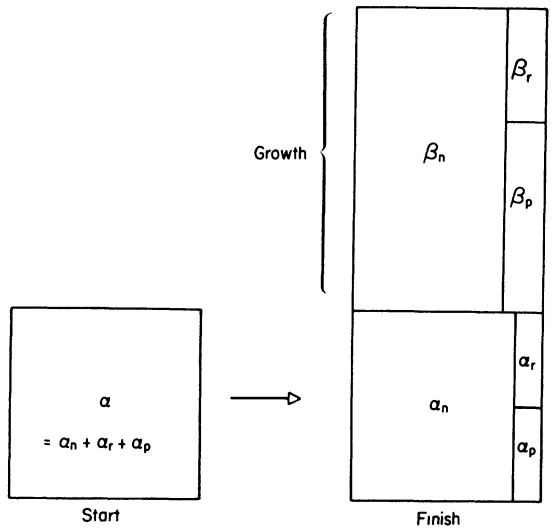

FIG. 1. Fractions into which weight may be apportioned. The part α is material present at the start of the growth period. The part β is growth during the period. Parts subscripted r are lost in respiration; those subscripted p are lost from other causes.

attack, physical removal by wind and water and, perhaps the most important, that due to microbiological attack. The net growth is then β_n. The quantity $\beta_n + \beta_p$ corresponds to the usual definition of net primary production.

It is probably true, in general, that $\alpha_n/\alpha \neq \beta_n/\beta$. This is partly because the original plant material is in a different environment (and a different biochemical state) from the new growth. In particular, the rate of loss of matter from dead *Sphagnum* is affected by its position relative to the water table (Clymo 1965). Nor are the ratios α_n/α and β_n/β constant with time. It is for this reason that the losses in this model are shown as amounts (which have dimensions and must be related to a particular time interval) rather than as dimensionless fractions. If long times are involved, β_p may come to be a large proportion of β.

If the results are presented per unit area, there is a good reason for using the sample size as unit. The interpretation of a result given as 10 mg cm^{-2} would be very different

from that given as 1 tonne ha^{-1}, though when reduced to a common area these are the same. The same argument applies to the unit of time, with the complication that there are here two conspicuous cyclic changes in habitat conditions (diurnal and annual), and interpretation may depend on knowing in what part of the cycle measurements were made. The obvious solution—using sample area and time as units—is not always possible. First, interest often lies in comparing results, and for this purpose a common unit is necessary. Secondly, for the *Sphagnum* work, almost all the estimates so far reported have been made on samples of undefined area, and have to be converted to an area basis. As a compromise, therefore, the unit of g dm^{-2} has been adopted, and where relevant the time given.

The ten methods which have been used for measuring growth of *Sphagnum* may, for convenience, be separated into four groups.

The first group contains methods which make use of an innate marker of time. The use of natural cyclic changes of branch length and spatial density of branches, and of [^{14}C]-dating, are examples.

In methods of the second group, reference marks are put outside the plants, and growth in length is measured against these.

In the third group, plants cut to a known initial length are used.

The fourth group contains methods in which direct estimates are made of change in weight over a period under the control of the experimenter.

The use of innate time markers

(a) Cyclic fluctuations may sometimes be found in the length of *Sphagnum* branches and in their spatial density. Similar cyclic fluctuations have been used to measure growth of the moss, *Hylocomium splendens* (Tamm 1953), and with more limited success *Thuidium tamariscinum*, *Ptilium crista-castrensis*, and *Pleurozium schreberi* (Tamm 1953), *Rhacomitrium lanuginosum* (Tallis 1959) and *Acrocladium cuspidatum* (Streeter 1965). In all these cases the cycle was shown, or assumed, to be annual. Cyclic patterns are conspicuous in other bryophytes too, for example, *Polytrichum commune*.

The causes of this behaviour have been examined by Hagerup & Petersson (1960), who state that most of the extension growth occurs in the autumn. Malmer (1962) figures *Sphagnum papillosum* showing three or four cycles, but carefully avoids describing them as annual. If these cycles are annual, they provide a simple method of measuring growth rate. The quantity measured is β_n (Fig. 1), or simply increase in length over a year. Where growth is rapid the method might be used over times shorter than a year.

Using this method Malmer (1962) found growth of about 3 g dm^{-2} $segment^{-1}$. The values of 2·3–9·6 g dm^{-2} reported by Pearsall & Gorham (1956), for 'standing crop' of *Sphagnum* for several sites in England were probably obtained with this method. In the present work the method has proved of limited value, for the reasons given below. In two cases, however, clear results were obtained. At Thursley Common, ten samples of 1 dm^2 of *S. recurvum* growing with *Juncus effusus* in a wet flush gave a mean value of 12 g dm^{-2} for the current cycle. The plants were harvested in December. *Polytrichum commune* close by, but in pure stand, gave a mean value (ten samples) of 8 g dm^{-2}. The other clear case was of *Sphagnum* growing in furrows ploughed 7 years previously at Coom Rigg, Northumberland. A minimum estimate of β_n over 7 years was available using the whole accumulated mass, but a more likely estimate was given by the cyclic branch pattern. The results are shown in Table 1. They are the more remarkable when

compared with estimates of 0·77 g dm^{-2} (Chapman 1965), for a mixture of *S. papillosum* and *S. magellanicum* about 300 m away.

In a few cases the cyclic change is of pigment density. An example is *S. rubellum* in some habitats in England. The red pigment, related to the anthocyanins, is an aglycone, production of which is increased at low temperatures (Rudolph 1964, 1965). The pigment is difficult to separate from the cell walls (Goodman & Paton 1954) and often remains conspicuous after other pigments have disappeared. An estimate of 2·7 g dm^{-2} for 'net annual production' of *S. fuscum* at one site in northern England was obtained by this means (Bellamy & Rieley 1967).

The principal advantages of this type of method are that there is no interference with the natural habitat before measurement, and the method is simple.

The main disadvantages are, first, that it is suitable for use only over a long time interval, unless the plants are growing very fast. Secondly, and more serious, it appears that in the English climate the cyclic changes in growth pattern are often not sufficiently marked for it to be possible to make clear separation of segments. Either the change occurs and is gradual, or no distinct change can be seen at all. There must always be some subjective element in deciding where a cycle ends, but Tamm (1953) judged the

Table 1. *Net annual growth in dry weight in furrows at Coom Rigg Moss, Northumberland, England*

Species	No. of samples	Minimum estimate (g dm^{-2} $year^{-1}$)	Probable estimate (g dm^{-2} $year^{-1}$)
Sphagnum papillosum	5	2·6	7
S. recurvum	15	3·2	9

For method of estimation, see text. The minimum estimate is an average of all material remaining after 7 years. The probable estimate is based on the current cycle of growth.

error in deciding where the boundary lay in *Hylocomium splendens* to be seldom more than 1–2% of the segment weight. By contrast in twenty-eight out of forty-two 1 dm^2 samples of *Sphagnum*, collected during the course of this work from a variety of sites in England, no cyclic fluctuations at all could be seen in more than three-quarters of the plants. The rate of extension growth is correlated, amongst other factors, with water table height (Overbeck & Happach 1956). It may be that the cyclic changes in morphology, and more particularly of changes sufficiently sharply defined to be of use, appear only where temperature or water supply (or both) show sharp seasonal changes. Hagerup & Petersson (1960) do, however, report a similar difficulty.

It is possible that some further growth may occur on a particular segment in the second or subsequent years. It seems unlikely that this is important, since Malmer (1962) reports, and such observations as have been possible here confirm, that all but the current segments have usually lost their green colour.

(b) In special cases, ^{14}C dated peat profiles may produce results which are interesting because they are averages over periods of several hundred years. It must be demonstrable that *Sphagnum* is the main constituent of the peat and, since dry matter content is not often published for ^{14}C-dated samples, assumptions may have to be made about this.

The quantity measured is β_n, over the time between samples.

As an example the data of Turner (1964) for Tregaron Bog may be used. Two samples from 169 to 171 cm depth gave dates of 2669 and 2624, each ± 110 years BP. A sample

from 82 to 84 cm gave a date of 2354±110 years BP. Turner writes 'The *Sphagnum imbricatum* peat between 82 and 171 cm, however, is very weakly humidified and differs little from a contemporary *Sphagnum* hummock; the leaves and branches, although brown rather than green, closely resembling those of a living plant. It is fairly uniform in structure . . .'. No dry matter contents are available but published values for peat are about 100±30 g litre^{-1} (e.g. Malmer 1962; Clymo 1965; Gore & Olson 1967). These data give a most probable estimate of 3 g dm^{-2} year^{-1} over a period of about 300 years, but the statistical errors in ^{14}C counting give limits for $P = 0{\cdot}05$ of 1–10 g dm^{-2} year^{-1}. The value of β or of $\beta_n+\beta_p$ over shorter periods would have been higher, though by how much is unknown.

The use of reference marks outside the plant

(c) Leisman (1957) measured the depth to a wire which was originally laid on the surface. Over 3–4 years the mean growth rate was 1·4 cm year^{-1} in the sedge mat zone of a bog in Minnesota.

(d) The disadvantage of a buried wire is that considerable disturbance is caused in locating it. This problem is largely avoided by using many separate cranked stainless steel wires (shaped like a car starting handle). One end of the wire, which can conveniently be about 10 cm long, is pushed into the *Sphagnum* carpet vertically (or parallel to the stems if these are not vertical). The horizontal section, about 1 cm long, is level with the capitula, whilst the free end, which must be of exactly known length, projects into the air.

The *Sphagnum* plants grow up around the vertical free end of the wire and the growth is measured from the amount of wire still projecting above the surface. The cross piece increases resistance to vertical movement of the wire among the plants. No decrease of growth around the wires has been observed in the 4 years that this method has been in use.

The quantity measured is an increase in length. To estimate β_n (Fig. 1), this length must be multiplied by the average mass of plants in unit depth of *Sphagnum* carpet. This point is considered later. The method has proved useful for annual measurements where the growth in length was about 2 cm.

It is difficult to test whether or not vertical movement of the wire relative to the plants occurs in spite of the cross piece. In Fig. 2 is shown a comparison of growth estimated by cranked wire with that estimated from growth of plants of known initial length. Agreement seems to be satisfactory, but the method must be suspect in very wet habitats, where the *Sphagnum* carpet is liable to move. In such situations the plants often grow almost horizontally and this method is then of little value in any case. The principal errors arise in the estimation of where the surface lies. They are least for the closely packed capitula on hummocks, and greatest in wet habitats. These errors may be reduced by using a glass tube, about 2 mm bore, with a perforated plastic disc 2 cm diameter fixed to the end. The tube, disc end first, is slid over the free end of the wire, and the disc serves to define the surface.

This method is simple, and can be used on a large scale. It has some disadvantages. The wires are often difficult to find unless a marker thread is used or detailed notes made locating the position to within 10 cm. The wires are also a potential hazard to grazing animals. Both these difficulties are reduced if the free end of the wire is doubled over and the top centimetre covered in coloured PVC.

Overbeck & Happach (1956), following earlier authors, used a thread tied round the stem as a marker against which to measure the growth in length of aquatic *Sphagnum* plants. They recorded growth of up to 44 cm between May and mid-October by *S. cuspidatum* growing in a ditch. They were unsuccessful in using this method in habitats which were not fully aquatic, because the monthly disturbance for measurements was too severe for the plants to survive. The plants tended to dry out, mainly because it was impossible to rearrange them after measurements in anything like the original grouping. Chapman (1965) used the same principle, but with only one disturbance at final harvest, to check that the stems below the markers were not lost. This method was tested during the present work. It involves more disturbance than the use of cranked wires, and was therefore abandoned at an early stage, even for situations where a single harvest was intended.

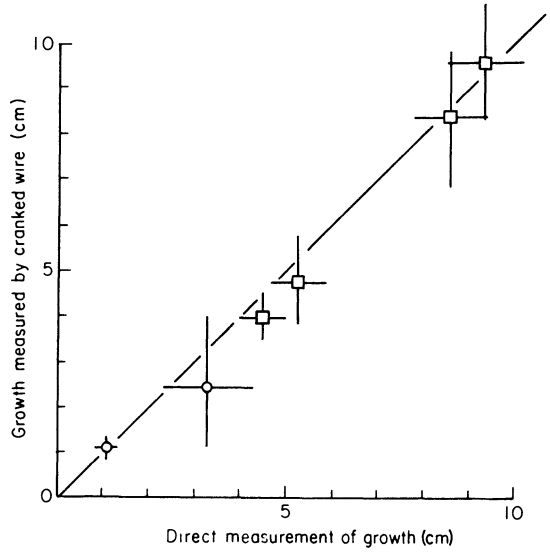

FIG. 2. Comparison of growth in length by direct measurement on plants of known initial length, with estimates by cranked wire. For details of methods see text. Values are mean of ten (containers near laboratory, □) or twenty-five (field, ○) measurements. Bars are ± twice the S.E. of the mean. The line of slope+1·0 is that on which the points would fall if the methods were in exact agreement.

The use of plants cut to known length

(f) Overbeck & Happach (1956) used cylinders of celluloid with a perforated base to contain *Sphagnum* plants cut initially to a length of 8 cm. The plants were removed at intervals, the extension measured, and the plants cut back to 8 cm and replaced in the cylinders. With such multiple removals, the growth may have been different from that of undisturbed plants, though there is no reason why the same procedure could not be used, but with only one harvest. Another potential error is due to the physical separation of the sample plants in the cylinder from the rest of the *Sphagnum* carpet. Whilst the water table remains above the base of the cylinder this may not be important, but one might expect it to become more so if the water table drops below the cylinder, though Overbeck & Happach did not see visible differences in plants inside and outside the cylinders.

As with other measurements of growth in length, conversion to growth in dry weight requires the use of values for spatial density and individual plant weight.

(g) Chapman (1965) used plants of *S. papillosum* and *S. magellanicum* cut to a length of 5 cm. Samples were taken for dry weight determination and the rest of the plants replaced in the bog surface. After a year, the extension and dry weight of the whole

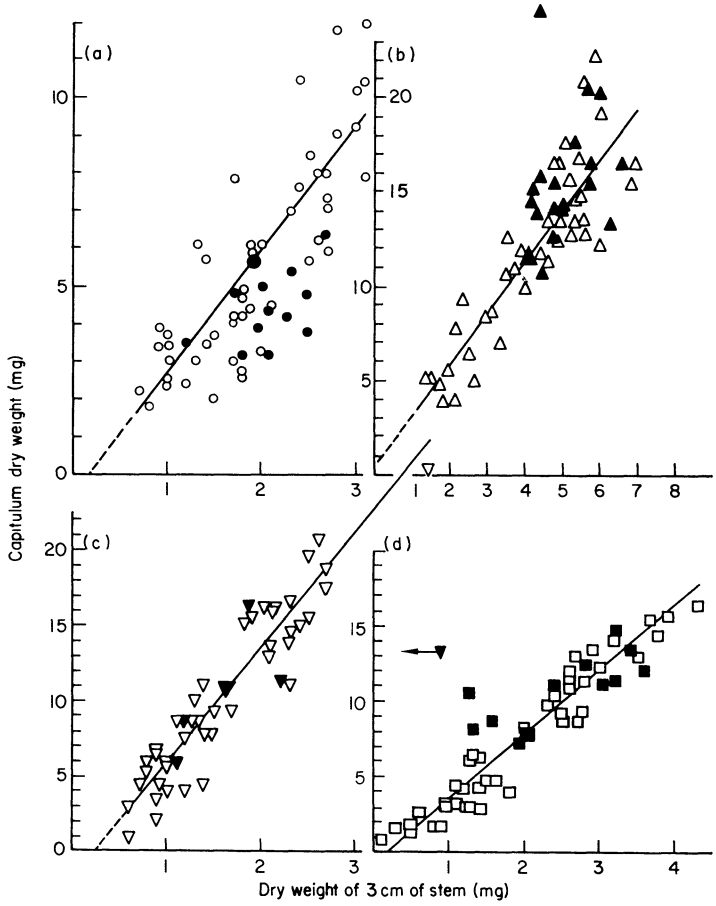

FIG. 3. Relationship of dry weight of capitulum to that of 3 cm of stem for four species of *Sphagnum*. Open symbols are values for a large sample of individual plants from the lot used in the container experiments. The calculated straight line of best fit for these points is shown. Filled symbols are mean values for other samples each from 1 dm^2. (a) *S. rubellum*: $y = 3{\cdot}25x - 0{\cdot}7$, $r = 0{\cdot}84$; (b) *S. papillosum*: $y = 2{\cdot}7x + 0{\cdot}4$, $r = 0{\cdot}89$; (c) *S. cuspidatum*: $y = 7{\cdot}6x - 1{\cdot}8$, $r = 0{\cdot}94$; (d) *S. recurvum*: $y = 4{\cdot}3x - 0{\cdot}9$, $r = 0{\cdot}97$.

plants were measured. Chapman reports that 'it was found that leaves and branches were lost from the bases of the shoots during the course of the experiment . . .' so that direct estimates of dry weight increases were unreliable. Marker threads showed, however, that whole pieces of stem were not lost, and '. . . increase in length provided a more accurate measure of growth . . .'. From growth in length, the growth in dry weight was calculated, using a graph relating dry weight to length. The increase in dry weight per unit area, β_n (Fig. 1), was then calculated using the mean spatial density of plants.

For small amounts of growth this estimate is, unfortunately, not very precise, because the growth is, relatively, a small proportion of the total weight and variability is large. (The coefficient of variation for weights of *S. magellanicum* 5 cm long was about 37% for a sample of twenty plants.)

(h) An obvious modification of Chapman's method would be to cut off and weigh the new growth directly. This may introduce errors, however, because some part of the material in the new growth has been carried there by internode extension; it is not *formed* during the growth period. The error will be largest where growth is small, and is large in many cases, where the capitulum may weigh 5 mg whilst the net annual growth is only 10–20 mg (Fig. 6). The easy solutions to this difficulty cannot be used because the capitulum itself may change size considerably, for example, when placed in a markedly drier or wetter environment than that in which it formed. The problem can, however,

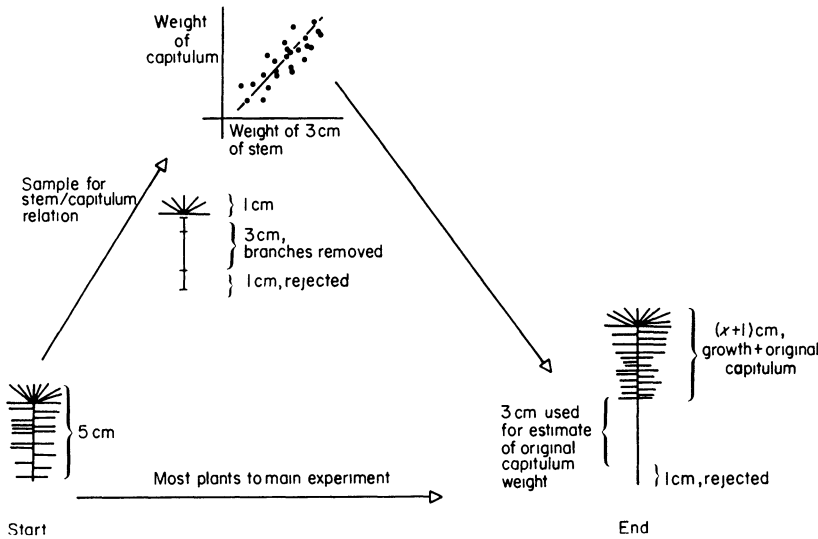

FIG. 4. The 'capitulum correction' method for measuring growth in weight.

be avoided using a rather more complicated technique. There is a fairly close relationship (Fig. 3) between the dry weight of the capitulum (defined for convenience as the top centimetre of the *Sphagnum* plant) and that of a unit length of stem, after the branches have been stripped off. From the weight of stem at harvest, an estimate may therefore be made of the capitulum weight at the start of the experiment.

The procedure used is shown in Fig. 4. The bottom centimetre of stem is rejected, because it sometimes becomes frayed, with the danger of losing small pieces. A check made with marker threads 1 cm from the bottom of the stem confirmed Chapman's (1965) observation that gross losses are rare; in five out of 200 plants marked in a field experiment the threads were not recovered at all after a year, and in a further six there was some loss.

The stems themselves lose weight slowly, so that if the correction for the original capitulum is large compared with the new growth, it is necessary to estimate the loss in weight of stems. In a field experiment these losses were approximately 5% in a year; this is smaller than the losses from whole plants (Clymo 1965).

Growth in both length and dry weight can be measured by this method. The dry weight increase estimated is β_n (Fig. 1). The assumption that there is no large amount of material translocated has proved difficult to check. There is certainly some movement of ^{14}C from older parts to new growth, probably outside the plant as $^{14}CO_2$. The reverse process seems to be of little importance. The method is sufficiently sensitive to make sampling at monthly intervals useful, although twenty-five samples, or more, are needed on each occasion.

Experiments to estimate the size of some possible errors are described later.

Although the relationship between capitulum weight and stem weight is usefully close to linear for a *particular* sample of plants (Fig. 3), there is considerable variation for samples from different seasons, habitats and localities. Without individual measurements for all these samples it is impossible to know whether the variation in mean values is due to differences in slope and position of the line, or to greatly different variances. Variances so different are unlikely, so it is important to take all the plants for a particular experiment from one area, and from the same habitat, and to determine the relationship for a sample of these in each gathering.

It is arguable that a polynomial, giving a better fit to the data, could validly be used here, because the object of this step is purely to estimate capitulum weight from stem weight. In practice the reduction in error variance by using even a second order polynomial is so small as to be not worth the extra trouble. The closeness of fit to a straight line through the origin is also useful because groups of plants of varying size may then be treated as units.

This method needs more work than most, but gives a fairly direct estimate of growth in dry weight as well as of growth in length. It can also be used in experimental (transplant) situations.

Direct estimates of change in weight

(i) The variability of weight for *Sphagnum* plants of equal length is so great that the obvious method of taking a sample of plants for dry weight measurement at the start of the experiment is imprecise, unless growth is several times the initial size. Estimates of total plant dry weight can be made from linear dimensions but, so far, no high correlation between dry weight and linear dimensions has been found.

A different approach is more successful. The plant is weighed first under water. A second weighing is made under water at harvest, and the plant is then dried and weighed a third time.

If specific gravity = d, weight under water at the start = W_s, weight under water at harvest = W_h, dry weight at the start = D_s, dry weight at harvest = D_h and growth = G, then

$$d = D_h/(D_h - W_h)$$

Assuming that d does not change during the experiment,

$$D_s = W_s d/(d-1)$$

and

$$\begin{aligned} G &= D_h - D_s \\ &= D_h(1 - W_s/W_h) \end{aligned}$$

The quantity estimated is $\beta_n - \alpha_r - \alpha_p$ (Fig. 1). This method is the most sensitive yet tested extensively; with care, growth of 2 mg may be detected.

There are several practical difficulties. Trapped gas bubbles must be removed from between the leaves, and from the hyaline cells. This is done by evacuating the plants

submerged in water. It is possible to 'boil' *S. papillosum* at 25° C for at least 1 min without serious harm to the plants: they continue growing afterwards. In normal practice only 5 sec evacuation is necessary. The effects of this treatment on subsequent growth are apparently very small (see tests described later). No trouble has been experienced from gas bubbles reappearing due to photosynthesis (though such bubbles are common in field conditions), and none should be anticipated if the weighing is made shortly after evacuation. Weighings must be made at a known temperature, and the plants allowed to reach this temperature before weighing. In this work 25° C was used.

If weighings under water are to be made directly then it is necessary to use either a balance completely immersed in water, or some form of suspension (between plant and balance) which passes through the water–air interface. It has proved difficult to build a completely immersed balance with the necessary precision (0·1 mg), range and robustness. The simpler solution, using an Oertling HO3 balance, with a cradle suspended in the

Table 2. *Specific gravity (at 25° C) of* Sphagnum

Species	Part and origin	No. in sample	Specific gravity	S.E. of mean
S. rubellum	Whole plants, end of experiment	48	1·65	0·009
S. cuspidatum	Whole plants, end of experiment	47	1·54	0·046
	New growth during experiment	24	1·55	0·040
S. papillosum	Whole plants, end of experiment	47	1·61	0·008
	New growth during experiment	24	1·62	0·014
	Whole plants from field	10	1·61	0·007
	Capitulum from field	10	1·60	0·012
	Stem 1–3 cm from field	5	1·60	0·021
	Stem 3–5 cm from field	5	1·63	0·018
	Branches + leaves 1–3 cm	5	1·62	0·010
	Branches + leaves 3–5 cm	5	1·62	0·031
S. recurvum	Whole plants, end of experiment	48	1·57	0·046

water was therefore adopted. The air–water interface produces a relatively large error in the balance reading, due to surface tension effects on the suspension. The observed weight may, however, be corrected for this error (see Appendix).

The validity of the assumption of constant specific gravity was examined in experiments described later: the results are shown in Table 2. There is no indication that the specific gravity of the new growth differs from that of the original plants, nor that there is any difference between parts of *S. papillosum*. There is some indication, though not significant at $P = 0{\cdot}05$, that the specific gravity of *S. papillosum* (1·61) and, particularly, *S. rubellum* (1·65) is slightly greater than that of *S. cuspidatum* (1·54) and *S. recurvum* (1·57).

It seems, therefore, that the basic assumption of the method is not seriously in error.

This method involves weighing the whole plant. Loss of branches, particularly from the lower part of the stem, is therefore a serious potential source of error. Because of this the method has not been tested in field conditions.

Stålfelt (1938) and Romose (1940) have measured changes in CO_2 concentration in a gas stream passed over moss plants in a closed container. It is also possible to use ^{14}C either in laboratory or field conditions. The problems of interpretation are, however, considerable, and are largely of a different nature from those of the other methods described here. They will not therefore be considered here.

'LABORATORY TESTS' OF SOME METHODS

The following tests were made in conditions in which the plants could be protected and the environment controlled. Field tests are described later.

Four species of *Sphagnum* were grown in opaque cylindrical polythene containers 25 cm diameter and 10 cm deep. The species were *S. rubellum*, *S. cuspidatum*, *S. papillosum* and *S. recurvum*. The unit for most measurements was a group of ten plants, but in some cases individuals were measured. All plants of one species were grouped together, the bundles being randomized, and surrounded by guard rows of plants on which no measurements were made. The plant axes were vertical and parallel.

The containers were put in a courtyard outside the laboratory. In two of them the water level was kept about 1 cm below the capitula and the top covered by nylon gauze

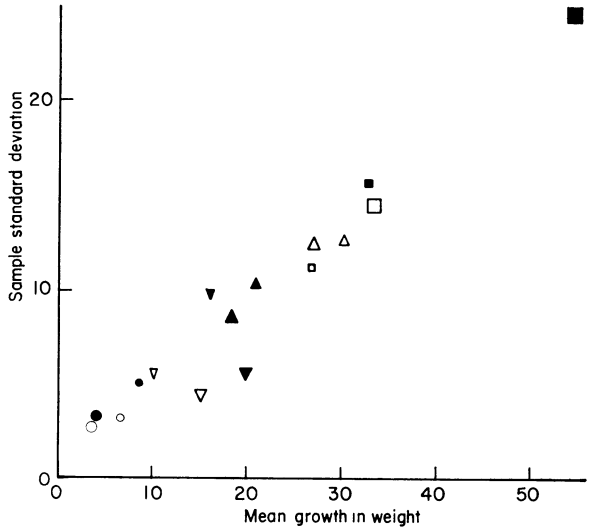

FIG. 5. Relationship between mean growth in weight (β_n, Fig. 1) and sample standard deviation, of plants grown in containers. Each sample contains forty individuals. Open symbols indicate estimates as mg plant^{-1}; filled symbols are estimates as mg (mg cm^{-1} stem)$^{-1}$; small symbols are for plants grown in drier unshaded containers; large symbols are for plants grown in wetter shaded containers. ●, ○, *Sphagnum rubellum*; ▼, ▽, *S. cuspidatum*; ▲, △, *S. papillosum*; ■, □, *S. recurvum*.

so that the radiation reaching the plants was, on average, about 30% of that in the unshaded containers.

In the two unshaded containers the water table was kept at about 5 cm below the capitula. These treatments were designed to produce differences in growth against which differences due to errors in the methods of measuring it could be compared. The orientation and position of the containers were changed randomly each week.

The experiments were begun in June 1965. One harvest was made in the first week of August 1965, and the main harvest in the first week of January 1966.

There were six main experiments in this series using three of the methods already described. For convenience these are referred to as the cranked wire (d), the capitulum correction (h), and the weight under water (i) methods.

The pattern of variation, and selection of a basis for expressing results

For each species and container forty plants were cut to 5 cm at the start of the experiment. At harvest in January the growth in length and in dry weight (by the capitulum correction method) were measured on individual plants. Results for the growth in dry weight are shown in Fig. 5. The growth is expressed per plant, and also per weight of unit length of stem. This last needs explanation. There is considerable variation in growth expressed per plant. The coefficient of variation (ratio of standard deviation to mean value) is about 0·5, which is undesirably large. This variation occurred both within a species and between species. It seemed that this might reasonably be related, to some extent, to variations in the growth potential of the plants. This growth potential could be related to the size of the apex, and the size of the apex is reflected in the size of the stem. In general, the larger the apex, the larger the capitulum and stem (Fig. 3). If growth were expressed per weight of unit length of stem one might hope therefore to reduce variability within species, and probably between species as well, though interpretation might then be more difficult. Such expression implies that the growth potential is approximately proportional to the cross sectional area of the stem and hence the cross sectional area of the apex.

In Fig. 5, comparison of the open symbols with corresponding filled symbols indicates that in general the coefficient of variation is similar for the two methods of expression. Indeed, there is a slight indication that the coefficient is actually greater if the results are expressed per weight of unit length of stem for plants in drier conditions. For practical purposes therefore, there is nothing to be gained by using weight of unit length of stem as the basis for expressing results. The immediate cause of this is the very low correlation between weight per unit length of stem and growth. This might be because growth potential is related to some function other than the square of the stem radius. The lack of correlation holds, however, even when the logarithm of the data is used (which might be expected to expose a power relationship if it existed). For example, the correlation coefficient (after transformation) for the forty plants of *S. papillosum* in drier conditions is as low as 0·09. It appears more likely that the explanation lies in the accommodation of apex size to the detailed conditions of its microenvironment, which will be the same as its original environment in the field only by chance. This suggestion is supported by the observation in the field experiments (described later) that the correlation of stem weight and growth is rather greater in the early stages after transplanting.

These results again lead one to suspect that the detailed microenvironment is important, and hence throw doubt on results from any method which involves repeated disturbance of the plants.

Another feature of the results in Fig. 5 is that, with the possible exception of *S. cuspidatum* in wetter conditions, the points all lie close to a single straight line; the error is proportional to the mean value. A logarithmic transformation removes most of this relationship, and reduces the coefficient of variation to about 0·15. All subsequent analyses have therefore been made on transformed data. Similar features are shown by growth in length, although the logarithmic transformation is not so satisfactory as for growth in weight.

The behaviour of the species in relation to water table (and shade) is very similar to that which might have been predicted from the field distribution of the plants: *S. rubellum* grew better in the drier containers, as did *S. papillosum* for which, however, the proportional difference was smaller. *S. recurvum* and *S. cuspidatum* grew better in the wetter

containers, even though these were also shaded. The difference was proportionally more marked for *S. cuspidatum*.

The effects of disturbance and of the 'weight under water' manipulations

All the plants were cut to 5 cm and weighed under water at the start of the experiment (June 1965). In each container three groups (of each species) were removed in August, re-weighed under water and replaced in the containers. Another trio was removed at the same time, the bundle of plants taken apart, then reassembled and replaced. A third set of three was not disturbed. In January all plants were re-weighed under water and after

Table 3. *Analysis of variance of growth in length and of growth in weight (bold figures) of* Sphagnum *subjected to three handling procedures*

Treatment	df	Mean square		*F*	
Handling (A)	(2)				
Untouched *vs* handled	1	0·16	**0·36**	0·5	**0·6**
Type of handling	1	0·22	**0·41**	0·6	**0·7**
Container (B)	(3)				
High water table *vs* lower	1	13·3	**14·6**	38·8***	**25·4***
Replicates	2	0·59	**1·2**	1·7	**2·1**
Species (C)	3	1·52	**34·7**	4·4**	**61***
Interactions AB	6	0·23	**0·29**	0·7	**0·5**
AC	6	0·58	**0·48**	1·7	**0·8**
BC	9	0·43	**0·80**	1·3	**1·3**
ABC	18	0·36	**0·52**	1·0	**0·9**
Error	96	0·343	**0·574**		

For details of treatments, see text. The logarithms of the original data were used in both analyses.

Table 4. *Mean values of growth in length, and of growth in dry weight (bold figures), of* Sphagnum *subjected to three handling procedures*

Treatment						
Handling (at first harvest)	Weighed		Separated but not weighed		Untouched	
	6·2	**8·6**	6·8	**7·6**	7·0	**9·0**
Container	High water table, shaded			Low water table, unshaded		
	8·7, 9·4	**5·4, 6·9**		4·5, 5·3	**11·9, 11·1**	
Species	*S. rubellum*		*S. cuspidatum*		*S. papillosum*	*S. recurvum*
	5·1	**3·2**	6·8	**4·3**	6·7 **14·5**	8·4 **25·0**

For details of treatments, see text. Growth in length is in centimetres. Growth in weight measured by method (h), is in mg plant^{-1}, without correction for losses during the experiment. Mean values have been re-transformed from logarithms.

drying at 105° C. Growth was calculated by both the capitulum correction and weight under water methods.

By January, many of the lowest branches of some groups of *S. cuspidatum* and *S. recurvum* had become separated from the stems in the high water table shaded containers and it was not always possible to associate the branches with the correct stems. Fortunately this did not affect the estimates made by the capitulum correction method and it is therefore in these terms that the results are given in Tables 3 and 4.

The analysis (Table 3) indicates that the handling procedures have a small effect compared with that of the water table and shading treatment, and with the differences between species. Handling tends to reduce growth.

The growth in weight of species in relation to water table (Fig. 5) is similar to that in experiment 1; it appears as the interaction BC but is of low significance.

Growth in length is consistently lower for all species in the drier containers.

Table 5. *Analysis of variance of growth in length, and of growth in weight (bold figures) of* Sphagnum *cut to different initial lengths*

Treatment	df		Mean square		*F*	
Initial length (A)	(2)	**(2)**				
3 cm *vs* 5 and 7 cm	1	**1**	0·11	**2·6**	3·6	**18·5*****
Rest	1	**1**	0·06	**0·17**	2·1	**1·2**
Container (B)	(3)	**(2)**				
High water table *vs* lower	1	**1**	4·04	**2·2**	140·2***	**15·7*****
Replicates	2	**1**	0·36	**0·59**	12·6***	**4·2***
Species (C)	3	**3**	0·27	**16·8**	9·4***	**121*****
Interactions AB	6	**4**	0·04	**0·15**	1·5	**1·1**
AC	6	**6**	0·05	**0·62**	1·8	**4·4****
BC	9	**6**	0·12	**1·4**	2·4*	**10·2*****
ABC	18	**12**	0·037	**0·34**	1·3	**2·4***
Error	46	**36**	0·029	**0·139**		

For details of treatments see text. The logarithms of the original data were used in both analyses. The comparison of 3 cm *vs.* 5 and 7 cm is undesigned.

Table 6. *Mean values of growth in length, and of growth in weight (bold figures) of* Sphagnum *cut to different initial lengths*

Treatment						
Initial length (A)	3 cm		5 cm		7 cm	
	5·8	**12·6**	6·0	**8·6**	6·4	**8·3**
Container (B)	High water table, shaded			Low water table, unshaded		
Species (C)						
S. rubellum	5·8	7·0	**2·2**	4·7	4·7	**6·9** **5·3**
S. cuspidatum	5·6	7·3	**2·5**	5·7	5·3	**2·7** **9·6**
S. papillosum	7·7	8·1	**22·0**	4·2	4·5	**22·0** **20·2**
S. recurvum	8·9	10·4	**26·2**	5·4	4·9	**22·7** **21·2**

For details of treatments, see text. Growth in length is in centimetres. Growth in weight, measured by method (h), is in mg plant^{-1}, without correction for losses during the experiment. Mean values have been retransformed from logarithms.

The effect of initial plant length on growth measured by the 'capitulum correction' method

The same four species and similar containers were used. One set of plants was cut to 5 cm long at the start of the experiment. Other sets were cut to 3 cm and 7 cm. All the capitula were arranged at the same level by supporting the shorter plants on a bed of homogenized *Sphagnum*. All were harvested in January. The plants from one of the high water table containers were lost before they could be weighed (during removal from one laboratory to another), so only the growth in length is available for them.

The results are shown in Tables 5 and 6. The effects of water table on growth in length and weight are similar to those in the other experiments, except for a high value for *S. cuspidatum* in one of the drier containers. No explanation is obvious; this may be a chance result.

There is some indication that the growth in length is inversely related to the initial length and quite strong indication that growth in weight is similarly related. The major part of the effect is due to greater growth by 3 cm plants. This is a result which was unexpected and is not easy to explain. For practical purposes 5 cm plants seem adequate, and have been used in the rest of this work, because 7 cm ones are not so easily obtained undamaged, and losses are more likely to occur from longer plants.

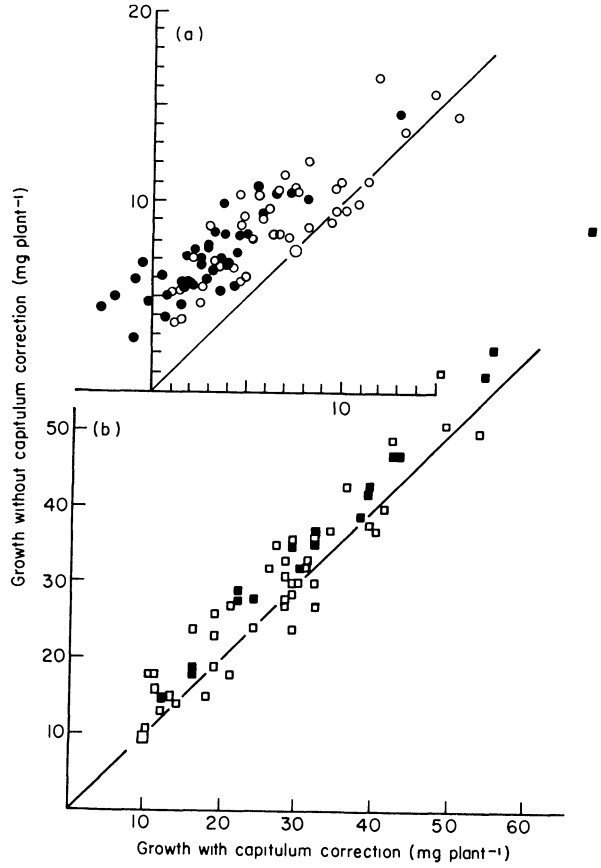

FIG. 6. Comparison of growth in weight (β_n) with and without correction for change in capitulum weight for two species of *Sphagnum*: (a) *S. rubellum* and (b) *S. recurvum*. The single large symbol in each graph is the mean correction value. Open symbols are for plants grown in drier unshaded containers; filled symbols are for plants grown in wetter shaded containers. The line of slope+1·0 is that on which the points would fall if the estimates were in exact agreement.

The effect of ignoring the capitulum correction

The same four species and containers were used. All plants were cut to 5 cm initially and were harvested in January. In addition to the usual separation at 4 cm from the base (Fig. 4) the section from 4 to 5 cm was cut off and weighed separately. It is thus possible to compare the growth estimated after capitulum correction with that estimated simply by removing everything beyond 5 cm. The results for two species are shown in Fig. 6. For *S. rubellum*, where the mean of the estimated initial capitulum size is about

half the growth, the difference between the estimates is considerable, and is larger the smaller the growth. For *S. recurvum*, where the growth was much greater, and averaged three to four times the capitulum weight, the difference is much smaller. The other two species fell between these extremes.

It is not, of course, demonstrated that the capitulum correction method is accurate; only that the methods give different results. It might be argued that the method cannot be accurate because it gives some negative results. This conclusion is not necessarily true

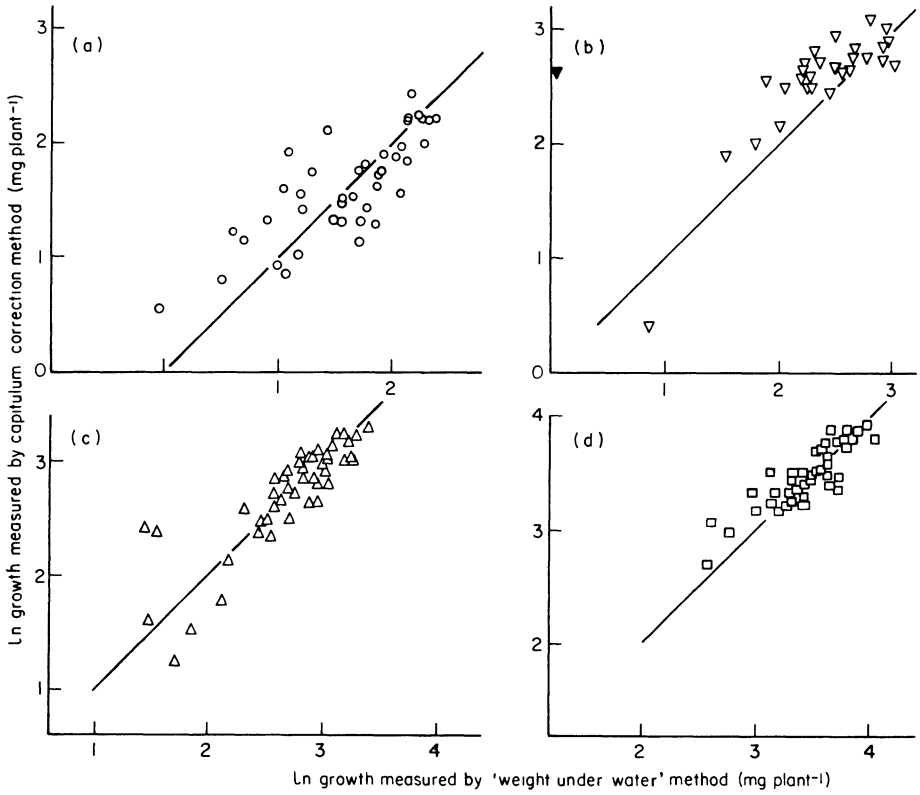

FIG. 7. Comparison of growth in weight ($\beta_n+\beta_p$) estimated by two different methods on the same plants. The line of slope + 1·0 is that on which the points would fall if the estimates were in exact agreement. For further details see text. (a) *Sphagnum rubellum*; (b) *S. papillosum*; (c) *S. cuspidatum*; (d) *S. recurvum*.

because no allowance has been made for losses ($\beta_r+\beta_p$), and some negative results must be accepted as the price of using a correction which relies on a statistical relationship which is not perfect (Fig. 3). The negative results could, however, raise a problem when using a logarithmic transformation. Fortunately this has not arisen in the present work since no negative values have been found with the capitulum correction method for groups of plants, although they do occur with individuals.

Comparison of growth in weight estimated by the 'capitulum correction' method with that from the 'weight under water' method

Plants from the handling experiment, together with some from a similar experiment not reported here, were used for this comparison. If the methods are to be compared

directly, some estimate must be made of the losses, particularly from the lower 5 cm of the plants, since one method estimates β_n and the other $\beta_n - \alpha_n - \alpha_r$. These estimates were made on dead (air dried) *Sphagnum* which was weighed before the experiment and then placed amongst the live plants. At harvest these plants were again air dried and weighed. It is assumed initially that the rate of loss was constant and applied to the average mass of material involved: the mean total weight at first and last harvest for the weight under water method, and half the corrected growth in the other. Losses are probably overestimated by this procedure, since they are likely to be different for live and for dead material.

The results are shown in Fig. 7, where the data have been transformed into logarithms. Some of the original data for the weight under water estimates were negative and could not be thus transformed. They have therefore been omitted. There were two such cases of *S. rubellum*, eight of *S. cuspidatum* and one of *S. recurvum*. This point is of some importance, since these negative values were for groups of plants *after* allowance had been made for losses. In these circumstances one would expect negative values to be rare and small. Those for *S. rubellum* could perhaps be accepted as due to cumulative small errors in measurement and loss estimates, since the growth was small. Those for *S. recurvum*, and particularly for *S. cuspidatum*, are less easily accepted however. The negative values (and the wildly deviant value for *S. cuspidatum* shown as a solid symbol

Table 7. *Comparison of growth in dry weight estimated by two different methods*

Species	No. of samples	Correlation coefficient	Mean difference of estimates	'*t*'	S.E. of mean difference	$P = 0{\cdot}05$ confidence limits
Sphagnum rubellum	41	0·80	0·028 (1·03)	0·52	0 053	(0·92) to (1·14)
S. cuspidatum	28	0·84	0·186 (1·20)	3·60**	0·052	(1·08) to (1·34)
S. papillosum	47	0·85	0·012 (1·01)	0·32	0·038	(0·94) to (1·09)
S. recurvum	41	0·86	0·071 (1·07)	2·83**	0·025	(1·02) to (1·12)

The methods used were the capitulum correction method (h) and the weight under water method (i). Data were transformed to logarithms for analysis. Values in parentheses are retransformed to the original units, and are therefore the ratio of the estimate by method (h) to that by method (i).

in Fig. 7) are not obviously associated with particularly small values of growth estimated by the capitulum correction method (which might have indicated that the logarithmic transformation was inappropriate for very small values). The simplest explanation of these features is that there is some gross error in some of the estimates by the weight under water method. The most likely is that gas bubbles were trapped between the plants during weighing. This is particularly likely to happen with *S. cuspidatum*, because the branches tend to flex over bubbles and prevent their release. Of the nine *S. cuspidatum* samples showing these large deviations, four were weighed at the intermediate harvest as well, and all show growth since the first harvest, but a large apparent loss between second and final harvest.

There is some indication that this may have happened to a few plants of *S. rubellum* and *S. papillosum* as well.

Assuming that the errors in each method are random, it is possible to calculate the difference between the two estimates for each sample and test the hypothesis that the mean difference is zero (Table 7).

There is no reason to suppose, from these data, that the two methods give different results when applied to *S. rubellum* and *S. papillosum*, for which the mean differences

are 3 and 1%. The agreement is less good for the other two species: 7 and 20% difference. Apart from the possibility of errors due to small gas bubbles (not large enough to produce gross anomalies) for which there is no real evidence, the most likely source of the discrepancy lies in the correction for losses, which is larger for these species than for *S. rubellum* and *S. papillosum*. The sensitivity of the estimates to changes in the value taken for proportion lost is not the same. For the weight under water method the correction must be applied to the average total mass, including the original plants. For the capitulum correction method, the allowance for loss is made primarily on the new growth (with a separate and less important correction for loss of original stem material). Where growth in weight is large compared to the weight of the original plant, the difference between methods is therefore relatively insensitive to errors in the estimates of loss, though the absolute value of both is, of course, altered. Where growth in weight is small compared to the weight of the original plant, the difference between methods is larger. *S. recurvum*, for which the ratio of growth to original dry weight was about 1·5, shows the first of these conditions; *S. cuspidatum*, with a ratio of about 0·3, shows the second.

The sensitivity to errors in loss estimates can easily be shown. It is possible to calculate the proportional loss necessary to make the sum of the difference between the methods equal to zero. For *S. cuspidatum* this is 0·28, compared with the value of 0·23 measured. For *S. recurvum* the loss would have to be 0·50, compared with 0·25 measured. It has been assumed that the losses were uniform in time and that they were the same for live and dead parts of the plant. These assumptions are almost certainly untrue, and add a further element of uncertainty. The sensitivity of the growth estimates for *S. cuspidatum* (by the weight under water method) to such a small change in estimates of losses is so great that the observed mean difference of 20% should probably not be taken to indicate that the two methods of growth estimation disagree, although when the errors in loss estimation are added they do. For *S. recurvum* there may be real disagreement, though the size of this is much smaller: 7%.

In conclusion, it seems that, if losses are large, or if growth is small, the weight under water method is particularly open to error, and great care must be taken to avoid trapped gas bubbles in all situations. If growth and losses are large, the two methods may agree, but the accuracy of the estimates of $\beta_n+\beta_p$ depends much more on the accuracy of loss estimation. In their general agreement the two methods mutually support the conclusion that both are fairly reliable—with the reservations already made. Since the weight under water method is technically more difficult and prone to accidents, the capitulum correction method is usually preferable, though less sensitive.

Comparison of direct and 'cranked wire' estimates of growth in length

These estimates were made on cranked wires in the containers and on the plants immediately around the wires. The results are shown in Fig. 2. Agreement was satisfactory.

'FIELD TESTS' OF TWO METHODS

Methods which are practicable in the protected conditions just described are not necessarily suitable in field conditions.

The main object of the following experiment was to test the capitulum correction method (h) and the cranked wire method (d) in field conditions. The tests were more

satisfactory than anticipated and gave results with wider application than expected.

The experimental sites were at Moor House National Nature Reserve, Westmorland, England (on the area, at about 575 m altitude, known to workers on the Reserve as Burnt Hill) and on the bog at Thursley Common, Surrey (at about 30 m altitude and now a local Nature Reserve).

Burnt Hill is covered by blanket bog. The experimental area is to the south of the centre. It is about 300 m across, very wet, and with a well-developed pool and hummock

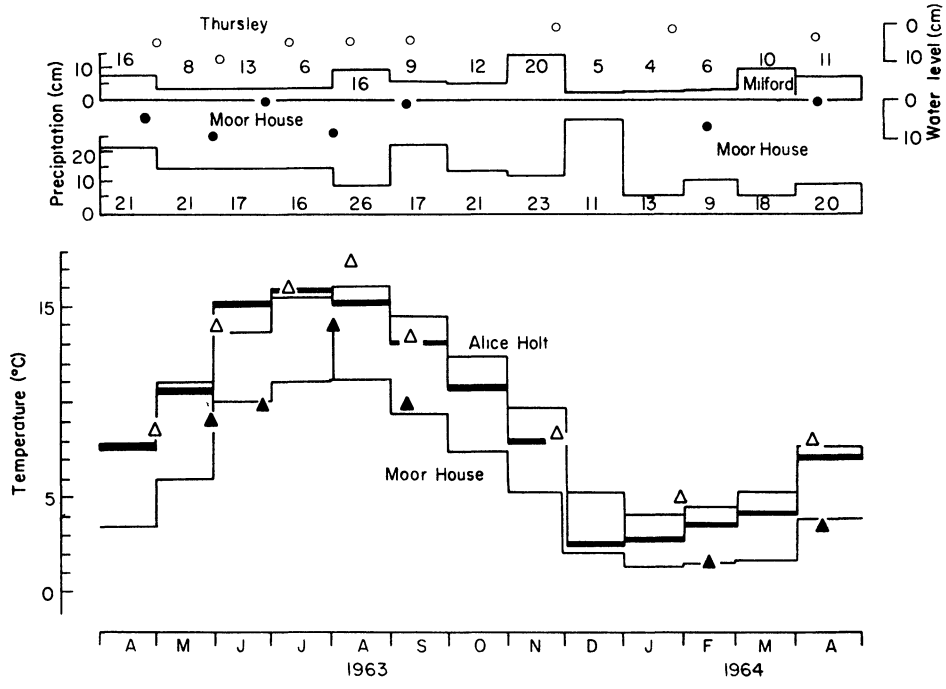

FIG. 8. Some climatic and habitat variables for the field sites, Thursley Common (Surrey) and Moor House (Cumberland). The lower histograms are monthly mean temperature. For Moor House, the temperatures were recorded at 09.00 hours daily at 30 cm in the ground about 1 km from the experimental site. For Thursley Common the nearest comparable records are from Alice Holt (Hampshire) about 13 km from the experimental site. Records are for 20 cm (thick lines) and 61 cm. Triangles are spot measurements on the experimental sites at 30 cm. The upper histograms are 'rainfall' at the same Moor House meteorological station as temperature and at Milford, about 4 km from the Thursley site. Figures in the histograms are number of days with more than 1 mm of precipitation. Circles show the position of the water table in the pool on the site, relative to an arbitrary datum.

complex (including hummocks of *Sphagnum fuscum*). The edges of the peat are eroding, with gullies as deep as 2·5 m. Bower (1959) considered that the hill is in an early stage of erosion, and that the gullies are cutting back into the central mass. The most abundant macroscopic plant species in the experimental area are *S. papillosum*, *S. cuspidatum*, *S. rubellum*, *Eriophorum vaginatum*, *E. angustifolium*, *Scirpus cespitosus*, *Empetrum nigrum* and *Cladonia arbuscula* (agg.).

Thursley Common is a valley bog, deriving its main water supply from a catchment of Lower Greensand (Folkestone beds). The surrounding area is dry heath, mainly

covered by *Calluna vulgaris*, *Erica cinerea*, *Betula* spp., *Pinus sylvestris* and *Ulex europaeus*. This bog is also very wet, and has probably grown considerably during the last hundred years, due to impeded drainage. Tracks shown on the 1870 (revised 1913) Ordnance Survey map as crossing one arm of the bog are now covered by up to 1½ m of peat. The experimental site lies in the other arm of the bog, in an area shielded from the main line of water flow, in a similar way to that described by Newbould (1960) for Cranesmoor—a New Forest bog. The peat in this area is about 90 cm deep. There are a number of pools in the area, but fewer hummocks than on the Moor House site. There is, again, an almost complete cover of *Sphagnum*, mainly *S. papillosum*, *S. recurvum* and *S. rubellum*. The pools within 20 m of the site contain rather little *S. cuspidatum*, but this species is common elsewhere. Fires are frequent on the surrounding heath, but do not appear to have affected the bog surface much.

Since this experiment was primarily to test the methods, only a few spot measurements of climatic variables were made. At harvest times a temperature profile to 30 cm and the water level in relation to a fixed post were recorded. At both sites the water table can fluctuate by at least 5 cm in 3 days. The maximum difference between spot measurements at Thursley was 8 cm, and at Moor House 9 cm. There is no obvious relationship (Fig. 8) between the spot levels and monthly rainfall. This is not unexpected since the water table fluctuates relatively rapidly. There is, however, a close connection between mean temperature at 30 cm and that at the meteorological stations at about the same depth, with the possible exception of higher temperatures in August in both bogs. The 30 cm depth was chosen as a depth at which some integration of the daily fluctuations of surface temperature would be achieved (Geiger 1965). The mean difference between sites is about 2° C or about 2 months in the year for a given temperature. The surface fluctuations of temperature are much greater of course; up to 30° C at the surface has been recorded on a sunny windless day even at Moor House, but in the absence of more detailed records this will not be considered further.

The species in the experiment were the same four as in the laboratory tests. They were all collected at Moor House, and cut to 5 cm long before replacement in the *Sphagnum* carpet at Moor House, or transplanting to Thursley. At each site, groups of plants were placed in each of three habitats. These could not be defined beforehand in terms of height relative to the water table, so the *Sphagnum* plants were themselves used as indicators, and the three habitats defined as pool (*S. cuspidatum* and *S. recurvum*), lawn (*S. papillosum* and some *S. recurvum*) and hummock (*S. rubellum*). There were six harvests through the course of a year (at 10, 14, 20, 30, 41 and 51 weeks) after the start in late April 1963. Transport difficulties precluded harvesting at both sites on the same day, but the interval was never more than a fortnight and mostly much less. For statistical purposes these harvests have been treated as contemporary. The harvested plants were stored at −16° C until it was convenient to measure them. (Storage at 2° C is not sufficient to prevent extension growth in some cases.)

The unit for measurements was a group of ten plants tied round loosely with a nylon thread, to help location and identification. Measurements were made of growth in length and in mass, by the capitulum correction method. Concurrent estimates of losses were made on dead *Sphagnum* in nylon bags (Clymo 1965), allowing an estimate to be made of the quantity $\beta_n + \beta_p$ (Fig. 1). The correction for losses was about 20% of growth, depending to some extent on species.

During the experiment three groups of plants were not recovered for a variety of reasons. They have been treated as 'missing plots' in the analyses (Snedecor 1956). A

Table 8. *Analysis of variance of growth in length and of growth in weight (bold figures) of* Sphagnum *in field conditions*

Treatment	df	Mean square		F (all ***)	
Time (A)	5	3·3	**4·0**	160	**66**
Habitat (B)	2	7·4	**1·1**	361	**19**
Site (C)	1	4·2	**5·6**	205	**93**
Species (D)	3	2·9	**15·4**	142	**255**
Interactions BC	2	0·33		16	
CD	3	0·42		21	
ABC	10	0·23		11	
Error	27	0·021	**0·060**		
Total	140				

For details of treatments, see text. Growth was transformed to logarithms in both cases. Only effects with $P \leqslant 0{\cdot}001$ are shown here.

Table 9. *Mean values of growth in length of* Sphagnum *in field conditions*

Sampling time (A) (weeks and approximate calendar date)	Habitat (B) Hummock (amongst *S. rubellum*)		Carpet (amongst *S. papillosum*)		Pool (amongst *S. cuspidatum*)	
Site (C)	Thursley	Moor House	Thursley	Moor House	Thursley	Moor House
10 Last week June	0·8	1·2	2·3	1·5	2·8	2·4
15 First week August	3·0	1·7	4·4	2·4	4·0	3·3
20 Second week September	3·5	1·9	4·6	3·4	5·5	5·4
30 Third week November	4·1	1·9	4·7	4·4	7·4	5·6
41 Last week January	3·2?	1·9	3·8?	3·7?	7·3	4·7?
51 Second week April	5·2	1·9	4·7	4·2	8·3	5·8

Species (D)	Site (C) Thursley	Moor House
S. rubellum	3·0	1·8
S. cuspidatum	4·8	4·0
S. papillosum	4·1	2·4
S. recurvum	4·3	3·8

For details of treatments, see text. Growth is in centimetres. Mean values have been retransformed from logarithms.

Table 10. *Mean values of growth in weight of* Sphagnum *in field conditions*

Sampling time (A) (weeks and approximate calendar date)	10 Last week June	14 First week August	20 Second week September	30 Third week November	41 Last week January	51 Second week April
	5·5	10·3	12·3	14·0	15·3	16·7
Habitat (B)	Hummock (amongst *S. rubellum*) 10·1		Carpet (amongst *S. papillosum*) 11·4		Pool (amongst *S. cuspidatum*) 13·7	
Site (C)	Thursley 14·2		Moor House 9·5			
Species (D)	*S. rubellum* 4·4	*S. cuspidatum* 15·3	*S. papillosum* 14·4	*S. recurvum* 18·7		

For details of treatments, see text. Growth is in mg plant^{-1}. Mean values have been retransformed from logarithms.

more serious problem, which has not been solved satisfactorily, is the sporadic occurrence of individual dead plants, and in six cases (out of 141) of whole groups of dead plants. All these were measured separately from the live ones. The sporadic dead plants were not obviously systematic in occurrence, so were left out, the growth per plant being corrected accordingly. The whole groups were more systematic; four were *S. cuspidatum* in the last three harvests in the drier habitats, and the other two were *S. recurvum* in the last two harvests, again on the hummocks. Absence of further growth of these species in dry habitats at the end of the experiment must not therefore be interpreted in the same way as for live plants.

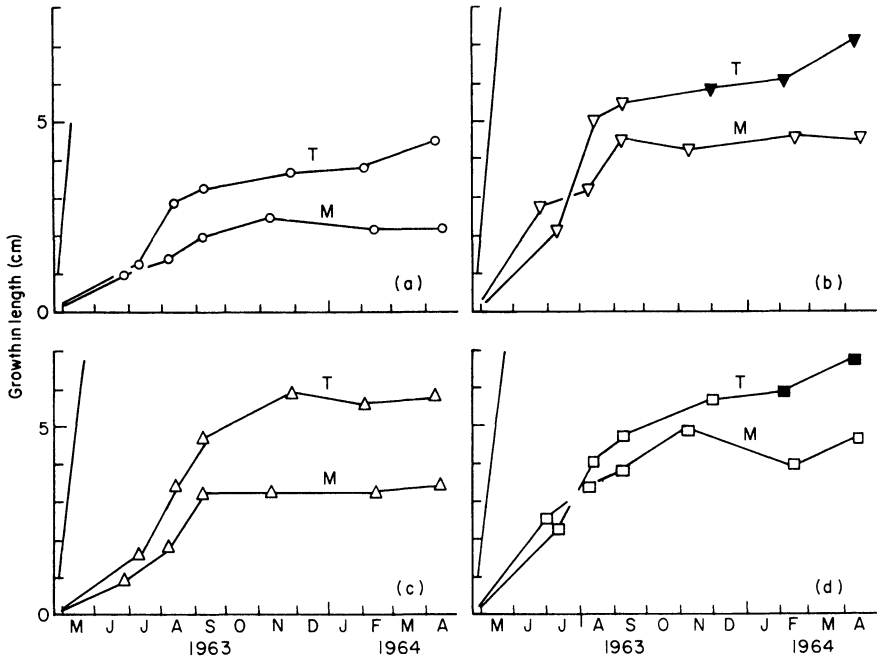

FIG. 9. Growth in length during a year for four *Sphagnum* species at two sites. The capitulum correction method was used. Filled symbols indicate that all plants at this harvest were dead. Data were transformed to logarithms for analysis, so the S.E. varies with the mean. As a graphic aid, the S.E. of the y value is shown (by the steeply sloping line) as a displacement from the $x = 0$ axis. The units of this are, however, those of the y axis. (a) *S. rubellum*; (b) *S. cuspidatum*; (c) *S. papillosum*; (d) *S. recurvum*. T, Thursley; M, Moor House.

Estimates of growth in length were also made at Moor House, using cranked wires (d).

Results are shown in Tables 8–10 and in Figs. 9–12. The main purpose of the experiment was achieved. With the exceptions already mentioned the capitulum correction method appears practicable for field use, though rather tedious.

The analyses of variance give three groups of results.

The first group includes all but one of the main effects for both measurements. The significance of these is high—variability was far less than had been expected. The estimate of error was taken from the highest order interaction, but the results are hardly affected if second and third order interactions are used. The second group include the main effect of habitat and three interactions in the length measurements. These are all

highly significant statistically, but because of the death of some plants may, in reality, be less important. The interaction ABC is mainly due to four of the results in the fifth harvest (Table 9). These are biologically very unlikely and there is reason to think that some at least of these measurements were mistakenly recorded 1 cm short. The remaining interaction, CD, is due principally to the difference in growth in length of the more terrestrial species, *S. rubellum* and *S. papillosum*, at the two sites. The third group are results of much lower significance, which need not be discussed.

The principal results are:

(a) Growth is greater (Figs. 9 and 11) at Thursley, which has a summer temperature on

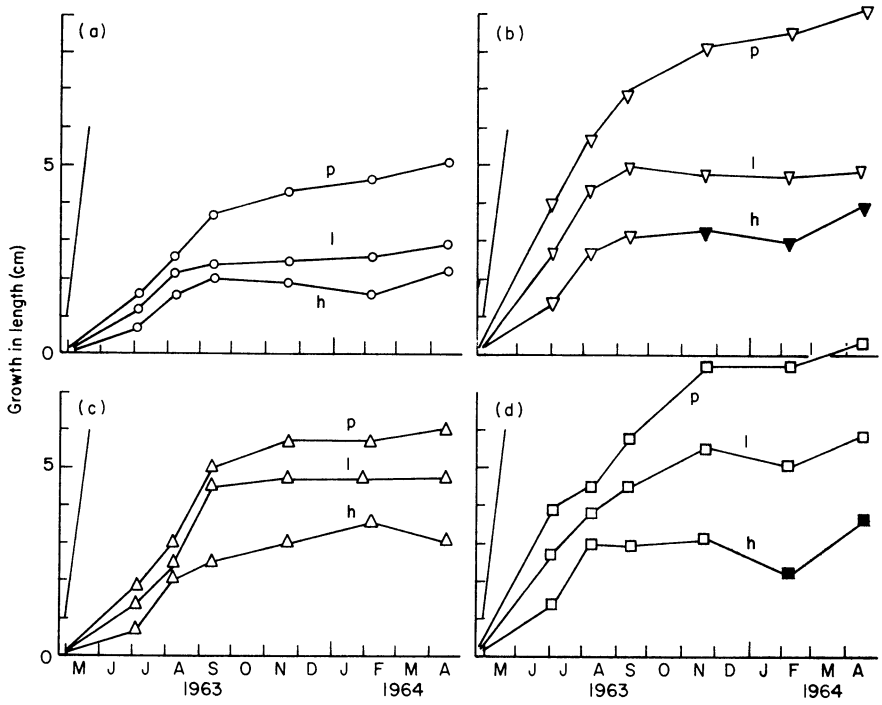

FIG. 10. As Fig. 9 but showing results for three habitats: hummocks (h) (with *Sphagnum rubellum* as original cover); lawns (l) (with *S. papillosum* as original cover); pools (p) (with *S. cuspidatum* as original cover). The harvest dates have been shown as half way between the actual dates at the two sites.

average 4° C higher than at Moor House, despite the higher rainfall and greater number of wet days at Moor House. Because of the hydrology of Thursley valley bog, the potential water deficit of the region is not manifested. In the absence of some system which amplifies and buffers the rain water supply, *Sphagnum* cannot survive in the present climate of the Thursley area, however. A set of ten estimates was made on *S. papillosum* at Moor House, but near the Stakebeck Mine at an altitude of about 750 m. These gave 12·5 mg plant^{-1}, compared with 23·6 mg plant^{-1} in a comparable habitat on the main site 175 m lower. The mean summer temperature for the Dun Fell meteorological station at about the same altitude and 3 km away is about 2° C lower than that at Moor House.

(b) The greatest growth rate occurs, as might be expected, in the summer months.

There is no indication of a midsummer 'rest period' such as that reported by Overbeck & Happach (1956). They worked, however, on a raised bog where the water table fell 20–35 cm in summer. In cultures with a constant water level, they found no such check in growth. The present sites were not subject to such extremes of water supply.

(c) It appears (Figs. 10 and 12) that growth in weight of plants in pools, particularly of species normally found there, continued during the winter months while other species, and these species in other habitats, had almost stopped growth. Temperature measurements in the pools might be informative.

(d) The difference of growth in weight in the three environments is least for the most terrestrial species (*S. rubellum*) and increases progressively to the most aquatic (*S. cuspidatum*). This may be interpreted to show that *S. rubellum* can grow well in a very

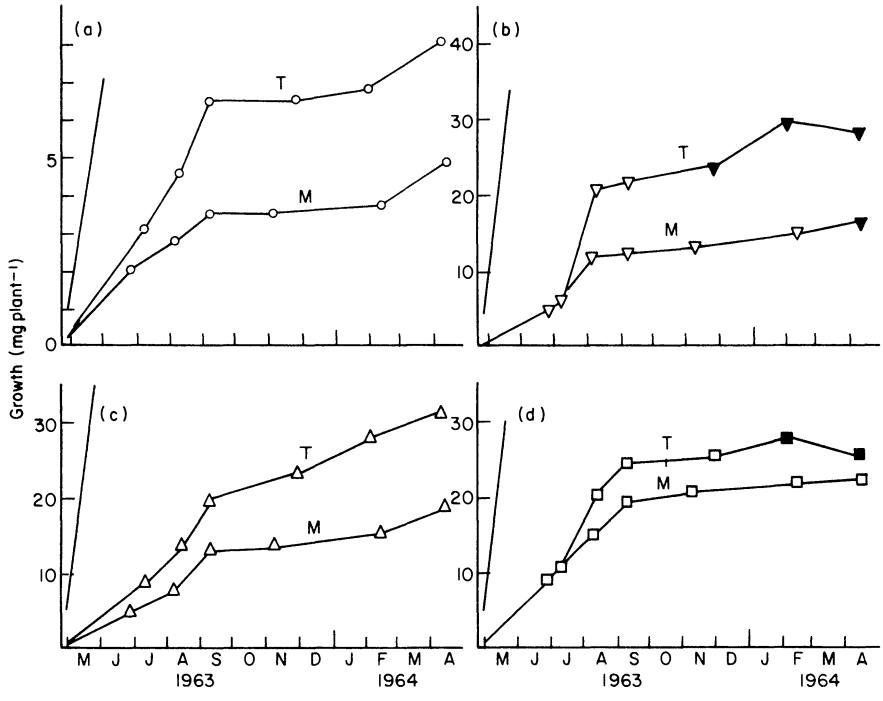

FIG. 11. As Fig. 9 but showing the net growth plant^{-1} ($\beta_n+\beta_p$, Fig. 1). (a) *Sphagnum rubellum*; (b) *S. cuspidatum*; (c) *S. papillosum*; (d) *S. recurvum*. T, Thursley; M, Moor House.

wet environment, though it is not usually found there, but *S. cuspidatum* cannot grow well in an environment much drier than it normally occupies. This is confirmed by the pattern of deaths already described. Growth in length does not show these differences to the same extent. Further comment on these factors will be made in a later paper.

Growth in length can be compared directly between different species. The difference *between* species of growth in length is least for the drier environment, and greater for the wetter ones. This has been confirmed in culture experiments, which are reported separately, and is best considered with them. The cranked wire and direct estimates (Fig. 2) are in satisfactory agreement.

It is difficult to compare estimates of growth in weight for different species, because they are expressed per plant, and the size of plants varies. A basis of unit weight of stem might be better, for reasons already discussed, but this unit is a highly specialized one. It is simpler to compare growth per unit area. The conversion from plant to area basis is now considered.

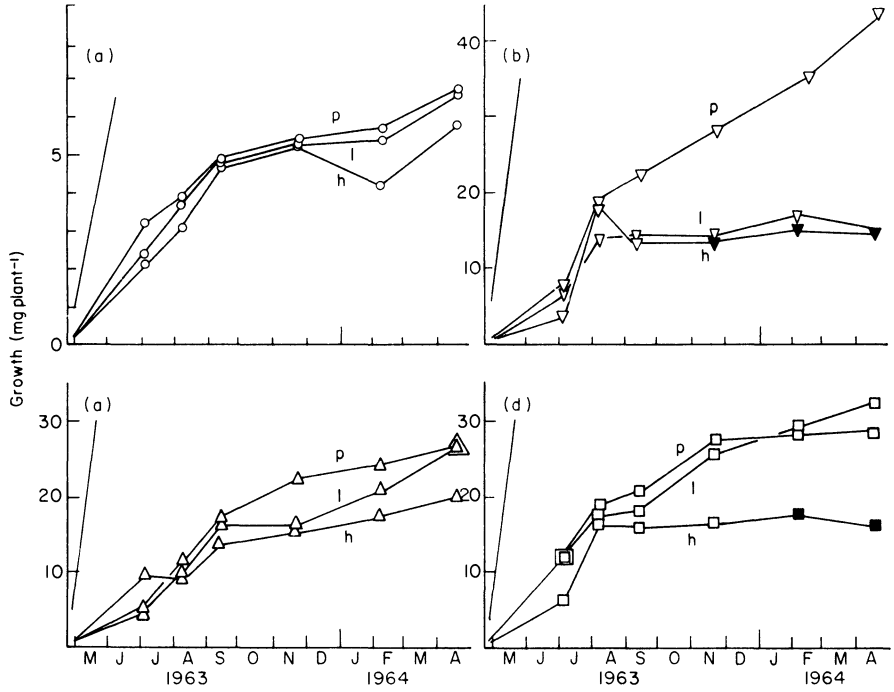

FIG. 12. As Fig. 10 but showing net growth plant^{-1} ($\beta_n + \beta_p$, Fig. 1). (a) *Sphagnum rubellum*; (b) *S. cuspidatum*; (c) *S. papillosum*; (d) *S. recurvum*. p, Pool; l, lawn; h. hummock.

CONVERSION OF RESULTS TO AN AREA BASIS

Sphagnum-dominated areas are often a mosaic of different species and habitats—for example hummock and hollow topography. Any estimate of production for the whole area will therefore need growth estimates on an area basis.

Overbeck & Happach (1956) estimated growth in length, the average number of plants/dm^2, and the dry weight of a length equal to a year's growth. Chapman (1965) used a similar method. Both report considerable variations, and unless the samples on which growth was measured occupy a well-defined area, a rather large error could be introduced. The relationship between numbers and average plant weight was therefore examined. All plants within square plots of side 10 cm were collected from a wide range of sites in England. The samples were required to be more than 95% of one species of *Sphagnum*, to contain few other plant species, and to be growing nearly vertically. They were taken from as wide a range of habitats as possible, not merely from the commonest one for that species. The number of plants in the sample was counted, and each plant was separated into capitulum (0–1 cm), and in most cases, the next 3 cm (1–4 cm).

Branches plus leaves were then separated from the stems, and the dry weight of these three fractions determined. In those cases where there was distinct periodicity in branch density and length, the whole of the segment was taken (instead of the arbitrary 1–4 cm section). All results are related to a unit of 1 cm length. Results for the same four species as before are shown in Fig. 13. The mean spatial densities reported by Green (1968) all fall within the limits shown here. The use of log numbers and weight leads to a very simple meaning attaching to the parallel diagonal lines with slope of -1. These are lines of equal mass area^{-1} depth^{-1}.

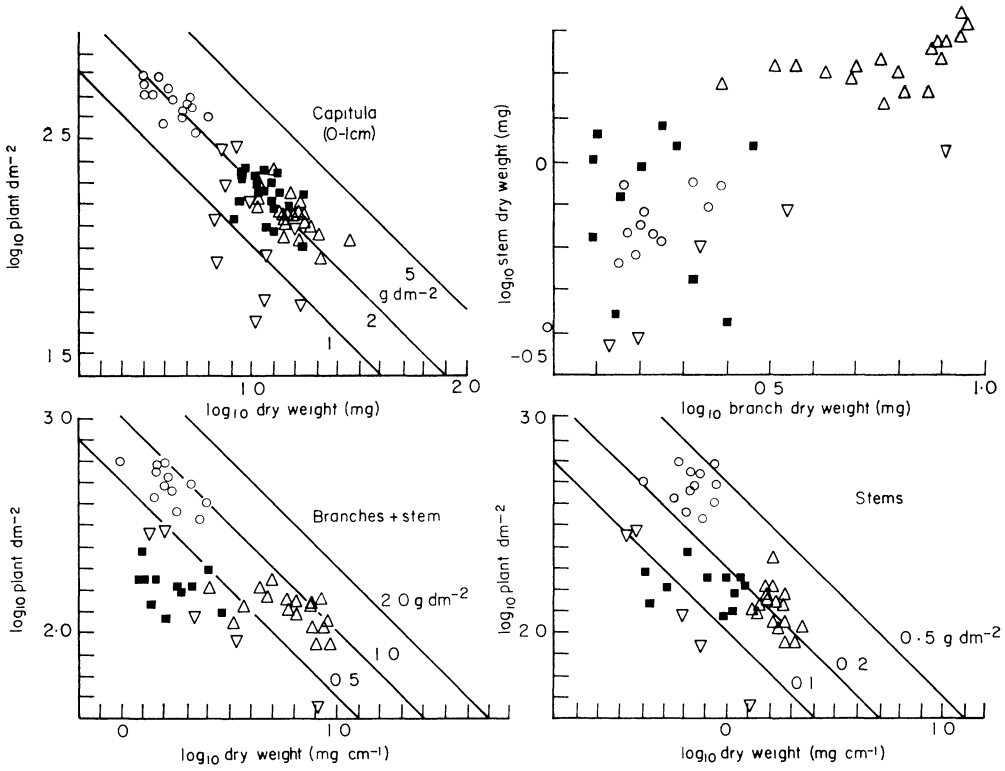

FIG. 13. Relationship between spatial density and mean dry weight per plant for various parts of *Sphagnum* plants, and between stems and branches of the same plants. ○, *S. rubellum*; ▽, *S. cuspidatum*; △, *S. papillosum*; ■, *S. recurvum*. Straight lines of slope $-1{\cdot}0$ are lines of equal weight dm^{-2} cm^{-1}. On some samples only the capitulum section was weighed.

There are several notable features in these graphs.

(a) Although it is in general true that the larger stems carry a greater weight of branches, the connection within a species is tenuous. This reflects the great variability in growth form. Some plants have many large branches closely packed, others with much the same size of stem have few branches widely spaced. These differences are found even in the absence of distinct cyclic variations.

(b) For all but *S. cuspidatum*, the mass dm^{-2} of capitula is remarkably constant. For *S. cuspidatum* the values are lower. This may be because it is rather uncommon to find this species growing much above the water table, or growing vertically. Even where the

vertical condition was satisfied the sites were usually very wet, and often the plants appeared to be spreading into a previously open site in very shallow water at the edge of a pool. The capitula were usually very lax, and the whole lawn very 'open' in structure.

Although the capitula are close to a constant mass area^{-1} depth^{-1}, the stems and branches are not. Each species has its characteristic region on the graph. The volumetric density of *S. recurvum* below the 'standard' capitulum is only about 0·3–0·5 that of *S. papillosum* and *S. rubellum*. This is almost exactly balanced, however, by the larger vertical extent of green branches. Where distinguishable on these samples, the depth of green canopy below the capitulum was on average 6 cm in *S. recurvum*, and only 2 cm in *S. rubellum* and *S. papillosum*. In all three species, the total mass of green branches plus stems is almost the same—2 g dm^{-2}—and the same as the mass of capitula.

It is not immediately apparent how this particular limit is imposed. Tinbergen (1940) and Overbeck & Happach (1956) have shown that more than 0·90 of the incident light (measured with a photocell) is absorbed in the top 2 cm of the *Sphagnum* lawns which they examined, although less for *S. recurvum* than for other species. The volumetric concentration of matter appears to be rather low (Table 11) but is not so when compared with most plant communities, which spread their photosynthetically active parts through a greater vertical range than does *Sphagnum*.

Table 11. *Volumetric concentration of matter in blanket bog at Moor House*

Depth (cm)	Dry weight (g l^{-1})	ml organic matter l^{-1}
0–1	20	12
1–4	10	6
45–50	120	75

Specific gravity = 1·6 has been used in the calculation. The data for 0–4 cm depth were taken from Fig. 13, those for 45–50 cm from Clymo (1965).

(c) For converting growth results to a unit area basis, the quantity required depends on the method. If growth in weight per plant is measured, then the spatial density is needed. For all but *S. cuspidatum* the standard error of the mean value of spatial density is about 10% of the mean value. If however growth in length is measured then the weight of plants per unit area and depth of lawn are needed.

The appropriate quantity is the 1–4 cm section rather than the capitulum, because the capitulum may be considered as the machinery which produces a continuous product—the stem and branches. The quantity required is the amount of product, not the amount of machinery. The standard error of the mean for the standard 3 cm depth of this measurement is also about 10% of the mean. (The scale on the diagonal axis of Fig. 13 is only 0·7 that of the vertical and horizontal ones.) Use of this conversion assumes that there has been no change in the size of the capitulum during the experiment, and for this reason alone must often be inaccurate.

More serious is that weight area^{-1} is not constant with depth—the extreme example is cyclic pattern of branch spacing. For periods of less than a year there may therefore be serious errors in assuming it to be constant.

The other major inaccuracy is likely to occur when the field data are applied to experimental situations. A plant may survive for a year in an experiment, in conditions in which it would not naturally form a community. In these circumstances the field data are used outside their range of application. Whilst the spatial density of plants can be

controlled, the morphological responses can not. It seems therefore that the first method, needing only the spatial density for conversion, is open to fewer objections than the second, though the second is the one which has been used by previous workers.

Results ($\beta_n + \beta_p$) from the last harvest of the field experiment have been converted to an area basis by both methods and are shown in Table 12. An analysis of variance on the logarithms of the differences shows some indication of a difference between the species, mainly due to the larger estimates by the first method for *S. cuspidatum* and *S. recurvum*. The mean difference for all is 9·5%, with a standard error of about 8%, but if there are large errors in the conversion from growth in length, as the differences between Figs. 9 and 11, and between Figs. 10 and 12 would suggest, then the lack of significant differences is entirely coincidental, and due to the positive and negative errors being of approximately equal size in the particular range of conditions used.

Table 12. *Estimates of growth (g dm^{-2} year^{-1}), by two methods for four species of* Sphagnum *at two sites and in three habitats*

Species		*S. rubellum*	*S. cuspidatum*	*S. papillosum*	*S. recurvum*
Habitat	Site				
Hummocks	Thursley	**4·3** (3·7)	**3·6** (3·4)	**3·1** (4·6)	**3·6** (3·2)
	Moor House	**2·4** (1·3)	**1·8** (1·2)	**2·4** (1·9)	**2·3** (1·1)
Lawn	Thursley	**3·2** (3·6)	**3·6** (2·6)	**4·0** (5·1)	**4·8** (2·6)
	Moor House	**2·4** (2·3)	**1·9** (2·3)	**3·3** (4·4)	**4·8** (3·3)
Pool	Thursley	**4·3** (6·8)	**7·9** (5·0)	**6·1** (8·2)	**5·4** (4·4)
	Moor House	**2·4** (3·8)	**7·9** (4·1)	**2·1** (4·5)	**6·0** (4·1)
No. of plants dm^{-2}		450	150	125	150
Mean g dm^{-2} cm^{-1} (stems + branches + leaves)		1·0	0·5	1·0	0·5

Estimates are made on plants from the last harvest only, from growth in weight per plant times mean number per unit area (bold figures) and from growth in length per plant times mean weight per unit area per unit length of plant (figures in parentheses). The constants for *S. cuspidatum* have been assumed the same as those for *S. recurvum*.

In summary, there is no strong statistical indication of differences, but if one method has to be preferred for experimental work it should be the capitulum correction method, as there are fewer objections to it. Using this estimate the results in Table 12 fit the usual ecological distributions of the four species. Although all species show greatest (or equal greatest) growth in pools (with the exception of *S. papillosum* at Moor House), the two species showing best growth in the different habitats are:

Hummocks	*S. rubellum* and *S. papillosum* (Moor House) or *S. recurvum* (Thursley)
Lawn	*S. papillosum* and *S. recurvum*
Pool	*S. cuspidatum* and *S. papillosum* (Thursley) or *S. recurvum* (Moor House)

Here, apparently, is another case where any explanation of field behaviour must include some consideration of plant interactions.

GENERAL DISCUSSION

The accuracy of growth estimates

As already mentioned, the only available evidence of accuracy is indirect and comes from the closeness of agreement between methods as diverse as possible. For this reason

the general correspondence (to within 20% or less) of the capitulum correction and weight under water methods, used in widely different habitats, is important. Additional support, though of much less value because qualitative, comes from the agreement between field growth rates and ecological behaviour.

Direct and indirect (cranked wire) estimates of growth in length are also in good agreement, but there are larger differences (individually up to 100%, though averaging 10%) for estimates on an area basis derived from capitulum correction and growth in length methods.

Taken together therefore, it seems that there is at least indirect evidence that estimates of growth by these methods are fairly accurate.

The constancy of total capitulum mass per unit area

Where w = mean weight plant^{-1}, d = number area^{-1}, and c and k are constants, then the equation for a straight line on Fig. 13 is:

$$w = cd^k$$

$$\text{or } \log w = k \log d + \log c$$

In this particular case $k = -1{\cdot}0$, and c = total mass area^{-1} cm^{-1}. There is a formal similarity between this result and those of Donald (1951) for *Trifolium subterraneum* and of Harper (1961) for *Bromus rigidus* and *B. madritensis* (both separately and in mixtures), at the stages in growth after the plants began to interact. There are, however, important differences in the conditions in which this relationship held for the higher plants and those for *Sphagnum*. The higher plants started at different densities, and had grown for the same time, and in the same environment. The plant weight was measured, with no limitation on the amount of vertical growth, whilst the *Sphagnum* measurements refer to the arbitrary depth of 1 cm.

Yoda *et al.* (1963) have shown that for four species of herbaceous weed and for four species (or groups) of forest tree in natural populations the value of k approaches $-1{\cdot}5$. In all cases the initial densities were probably so high that all stands, whatever their age or habitat, were self thinning, and at their limiting density for the particular mean size of plant.

If s = mean area covered by a plant, then

$$s = d^{-1}$$

Their second assumption is that the plants were, at all stages of growth, geometrically similar. The weight of a plant (assumed proportional to its volume) varies with l^3, whilst the area covered is a function of l^2. Hence:

$$s \propto w^{1{\cdot}5}$$

and so $k = -1{\cdot}5$ rather than $-1{\cdot}0$. For this to be true the less dense stands, with larger individuals, must also have larger vertical dimensions (though a similar result would follow if the volumetric density of plant material increased while the geometry changed). For example, their measurements on *Amaranthus retroflexus* show that the ratio of heights in least dense and most dense stands ($\simeq 30$) was more than the ratio of $s^{0{\cdot}5}$ ($\simeq 6$) for these stands. Taking an (arbitrary) fixed depth, as has been done with the *Sphagnum* measurements, is not consistent with the second assumption of Yoda *et al.* (1963).

It is difficult to devise a means for making the necessary measurement on *Sphagnum*; at least it would involve finding how many of the present capitula originated from the same plant. The appearance of a recognizable mutation or similar change seems to offer

the best possibility, but has not so far been reported. At one extreme a whole carpet might be the result of vegetative spread of one plant. The other extreme, with each present capitulum the direct and only product of each original plant, seems very unlikely, since forking of main stems occurs commonly. In experiments forking occurred significantly more often in drier conditions, and less often in *S. acutifolium* than in the other three species.

The fact that capitula of the three species of drier habitats have the same value for c ($\simeq 2$ g dm^{-2} cm^{-1}) is not surprising, since each can grow in the habitat normally occupied by the other, as the field experiments have shown, and the similarities in structure and behaviour of all three species are perhaps reasonably supposed to be more important than the differences. They are presumably, therefore, interacting strongly in natural conditions.

The rate of peat accumulation

Although the current rate of dry matter addition at Thursley is greater than at Moor House, it cannot be concluded that peat accumulation is more rapid. The rate of loss of matter from dead *Sphagnum* is also higher at Thursley (Clymo 1965). Nevertheless, the net addition of matter at the surface is greater at Thursley (Fig. 11), but the surface layers of live plants form only a small proportion—probably less than 1%—of the mass of peat at these sites. Not only is there a much greater depth of peat than of live plants, but the volumetric density is greater in the peat (Table 11). Even though the rate of loss of matter from the peat is lower by perhaps a factor of 100 than from the surface layers, the overall balance may be much affected by it. The present direct estimates of losses from the lower peat are not sufficiently precise or accurate (Clymo 1965) to allow any firm conclusion to be drawn.

The efficiency of a Sphagnum *carpet*

There seem to be two main uses of the term efficiency. In both the result of a process is considered.

First, and more strictly (Slobodkin 1962), efficiency is used to measure the ratio of output to input in a process. The same thing is measured at both input and output, so efficiency in this use has no dimensions. Examples are common in energy flow studies; growth efficiency, food chain efficiency, ecological efficiency (Phillipson 1966). In a disguised form the same concept appears in measures such as generation time (time for numbers out to become twice numbers in).

The second use is more general. Again the effectiveness of a process is described, but instead of input, some measure of the 'machinery' or capital is used. The dimensions in this case may be almost any. Examples of this use are growth as g dm^{-2} year^{-1} (dimensions m l^{-2} t^{-1}), where the capital is area and time, oxygen production per unit mass of chlorophyll (which is fundamentally dimensionless, although it could be expressed as l^3 m^{-1} at a given pressure and temperature). This second use grades imperceptibly into measures which are not usually thought of as efficiencies at all; spatial density (numbers per unit area, l^{-2}) is an example.

It is usually possible to make more than one measure of efficiency for a process, and there is no reason why efficiency in one set of terms should be correlated with that in another set (although it may be so). Efficiencies of different kinds cannot therefore be compared.

Table 13. *Efficiencies of* Sphagnum*-dominated and other communities*

Community	Place	Altitude (m)	Notes	Net production (t ha^{-1} $year^{-1}$)	t (P–kg)$^{-1}$ (% PO^4–P)	t (N–kg)$^{-1}$ (% N)	t (chl–*a*–kg)$^{-1}$	Reference
Sphagnum papillosum	Moor House	575	Lawn habitat	3				
Festuca–Agrostis grassland	Moor House	518	Above ground parts	1·9				Welch & Rawes (1965)
Calluna–Eriophorum	Moor House	550	Above ground parts	1·7				Rawes & Welch (in press)
Juncus squarrosus grassland	Moor House	550	Above ground parts	3·7				
Sphagnum papillosum	Thursley	30	Lawn habitat	4	2 (0·05)	0·1 (0·9)	2	
Pinus sylvestris	Brandon, Suffolk	< 50	Average for 17–55 years old	13	0·7	0·07		Ovington (1957, 1959)
Windermere Lake (North Basin)	English Lake District			0·5	(0·03)	(8)	1(2)	Lund, Mackereth & Mortimer (1963), Lund (1950), Talling (1965)

(1) P and N are for green parts of *Pinus* and *Sphagnum*, and median figures for *Asterionella formosa* Hass.
(2) Chlorophyll *a* (chl–*a*) in *Sphagnum* was estimated spectrophotometrically after grinding with $MgCO_3$ and extracting in 90% acetone at 5° C.
(3) Net production for Windermere was obtained assuming all C as CH_2O.

Efficiency is in most cases used as a practical and comparative tool. The measure selected must depend on the reason for making the comparison. In recent years two measures have been especially commonly used by ecologists. These are first, energetic efficiencies and second, efficiency based on area and time as capital. The energetic efficiency of *Sphagnum* is rather low. The energy content is itself rather low; 4·11–4·32 kcal g^{-1} (Gorham & Sanger 1967); 4·21–4·46 kcal g^{-1} for six samples of the four species used in this work. Radiation measurements have not been made at either site, but assuming 60 kcal cm^{-2} $year^{-1}$ for incoming radiation, the efficiency of *Sphagnum* is about 0·2%. On an area basis, at least in the upland site, *Sphagnum* seems to be of about the same efficiency, as a net dry matter producer, as the grasslands and drier blanket bogs of the area (Table 13). In the lowland site, net dry matter production (Table 13) is only about a third that of pine wood growing on sandy soil (Ovington 1957).

If comparison is made on basis of N or P capital employed, the position is altered (Table 13). In both cases *Sphagnum* has a higher efficiency than pine. That this may be a difference of biological significance is suggested by the work of Watt & Heinselman (1965) on the growth of *Picea mariana* on a bog in northern Minnesota, and of Brown, Carlisle & White (1966) on the growth of *Pinus sylvestris* on a bog in southern Scotland. In both cases there was a correlation between tree growth rate and foliar concentration of N and P, slow growth correlating with low concentration.

The uncertainties in comparisons of this kind, even those of what is nominally the same measure of efficiency, are considerable. They are, however, small compared with those which arise in attempting to compare the semi-aquatic with aquatic habitats. An attempt at this is shown in Fig. 13. On all bases there shown, *Sphagnum* appears to be more efficient than the lake, but differences by a factor of two cannot be counted important because of the difficulty in comparing an essentially evergreen community with one in which the number of live cells fluctuates so widely. Talling (1965) has produced concepts equivalent in many respects to those used in growth analysis of higher plants, which make comparisons between them possible. Unfortunately neither system can be applied easily to *Sphagnum*.

CONCLUSION

The results presented here show that the growth of *Sphagnum* is at least comparable with other communities from the same area. It seems desirable to know more about the field microenvironment and about the response of the plants. It is not possible, for example, to account satisfactorily for such obvious features of bog topography as hummocks and pools.

ACKNOWLEDGMENTS

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SUMMARY

Methods suitable for measuring *Sphagnum* growth over periods of a few weeks to several years are described.

Three of the most useful methods are compared in experiments; mean values agree to within 1–20% depending on species and habitat. Accuracy appears therefore to be satisfactory. Growth in length is not closely correlated with growth in weight unless referred to a particular environment.

The dry weight of capitula (defined as the top 1 cm of plant) per unit area is approximately constant—2 g dm^{-2} cm^{-1} for all species examined (Fig. 13). The total weight of green plant below this level also approximates to 2 g dm^{-2}, but there are differences in the depth to which the green parts extend.

Net production (Table 12) in a southern England valley bog at 30 m altitude averages about 4 g dm^{-2} $year^{-1}$, and in a northern England blanket bog at 575 m averages about 3 g dm^{-2} $year^{-1}$. Values differ by an order of magnitude for different species, habitats and time of year.

In general, growth in weight is greatest in pools, less on lawns and least on hummocks (Figs. 9–12). The difference between habitats is least for the hummock species (*S. rubellum*) and most for the pool species (*S. cuspidatum*).

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APPENDIX

Weighing objects which are submerged in water

If the object rests below water on a cradle, which is suspended from a balance in air by a wire which passes through the water surface, then two errors may be introduced in the weight recorded by the balance. The first applies only to those balances which use the amount of displacement from the zero position as a measure for the smaller subdivisions. (Usually this displacement is less than 2°, and is magnified by an optical system.) In such cases, as the beam at equilibrium is (usually) tilted relative to the zero position, then more or less of the suspension wire is submerged than would be if the

beam were not tilted. This affects the apparent weight, because some of the suspension wire previously in one fluid (air or water) is now in the other of different density. The error with an Oertling HO3 balance and two 26 SWG wire supports is 3·2% of that part of the weight covered by the optical scale: the third and fourth decimal parts of a gram (up to 9·9 mg maximum). This error can be calculated with sufficient accuracy.

The second error is much greater, and is due to surface tension forces on the wire at the air–water interface. If the water meniscus has reached equilibrium, and a known small weight is added to the beam so that the wire moves downwards, the meniscus is deformed, and the movement of the wire is opposed. The result is a smaller optical

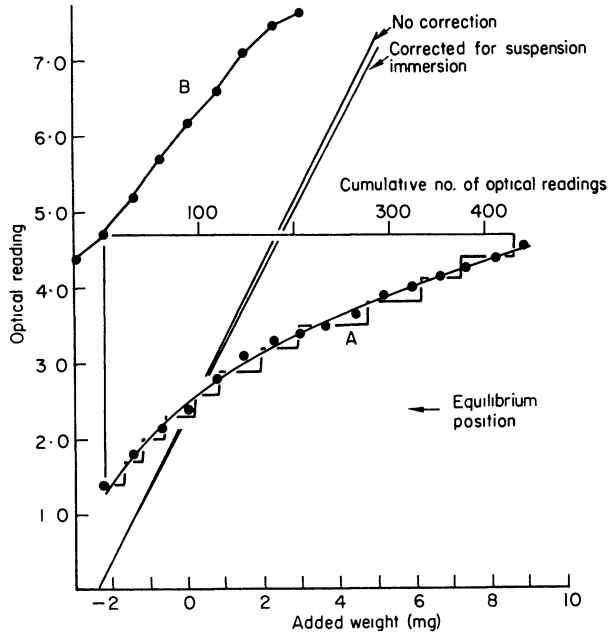

FIG. 14. Correction curve for immersion and surface tension errors in weight under water method. The two straight lines show the calculated effect of suspension immersion (see text), which is small compared to the experimentally observed deviations (●) shown by curve A and B (which is the continuation of A). The curve A through the experimental points is the calculated cubic equation of best fit. The histogram shows the cumulative frequency of weights of unselected objects (see text).

reading than expected. A similar error is produced if the beam rises due to removal of a small weight. These errors can be more than 100% of the optical part of the weight. Since total weights of about 50 mg have to be measured this error cannot be ignored. It can be reduced by putting soap or detergent in the water, but this seems undesirable when the plants are intended to continue growth. A surface coat of PTFE over the wire also reduces the error, but is mechanically unstable. One solution is to accept a relatively large empirical correction of the optical part of the weighing and to standardize the procedure carefully. As part of this procedure the wire suspension is cleaned frequently with acetone, and the water surface swept with paper. The empty cradle is weighed at least every fifth weighing to check for any sudden changes.

The detailed manipulations are designed to ensure a reproducible meniscus shape, and

to ensure that optical readings are made with the minimum departure from equilibrium. The procedure is:

(1) Set optical zero adjustment to a standard position. This is done because the optical reading is to be used as a measure of the linear displacement of the meniscus, not directly as an estimate of weight. The standard optical zero position used in this work was a reading of 5·0 at the point where the beam just rested on the knife edges.

(2) Find the approximate weight.

(3) Add about 20 mg too little counterbalancing weight and release the beam. The beam first moves down 0·3 mm without tilting until it rests on the knife edges, the meniscus being thereby depressed but not sliding up the wire. The beam then tilts and about 0·5 mm more of the suspending wire passes below the water surface, the meniscus sliding up the wire.

(4) Arrest the beam. This removes about 0·8 mm of wire from the water and leaves the meniscus extended. Steps 2 and 3 ensure that the meniscus is in a reproducible state before the weighing is made.

(5) Add the correct counterbalance weights and release the beam. With the particular balance used, the correct weights are such that the optical reading is between 1·4 and 4·6 (curve A, Fig. 14). As the beam is lowered, the meniscus is depressed by 0·3 mm. As the beam tilts towards lower optical readings, the meniscus is extended again, and (in these conditions) is at equilibrium at an optical reading of 2·4. At this point the curve relating optical reading to weight should be steepest, and a change of 0·1 units should be approximately equal to 0·1 mg. Careful examination of Fig. 14 shows that curve A is indeed S-shaped in the region of optical reading 2·4, though if the expected 0·1 mg = 0·1 unit relationship is present it must be so for a range of $\pm 0{\cdot}5$ mg at most. For practical purposes the third degree polynomial of best fit, which is shown in Fig. 14, was used. A check on this curve is provided by a Monte Carlo method: the cumulative frequency of 432 optical readings made during the experiments is shown superimposed on curve A in Fig. 14. The histogram follows the measured points with satisfactory exactness.

In many cases a second optical reading (curve B) may be obtained for the same object on the cradle by adding an extra 10 mg counterbalance weight. The meniscus is, however, in a very unstable state, and reproducibility is very poor. The region between 4·6 and 7·5 is therefore of no practical use.